

AN EXTINCT SPECIES OF *LEIOCEPHALUS* FROM HAITI (SAURIA: IGUANIDAE)

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Abstract.—At least five species of the endemic West Indian lizard genus *Leiocephalus* are known only by fossils excavated from cave deposits in the Greater and Lesser Antilles. Fossils of yet another extinct species were recently found in a crate of matrix that was collected over 50 years ago from caves near St. Michel de l'Atalye, Haiti. This new form, *L. anonymus*, has a partially closed Meckelian groove, a condition structurally intermediate between the fully open groove of the extinct species *L. apertosulcus*, and the completely closed and fused groove characteristic of all other living and fossil species of *Leiocephalus*.

One of the first assemblages of fossil vertebrates reported from the West Indies came from cave deposits in north central Haiti, northeast of the town of St. Michel de l'Atalye in the Département L'Artibonite. Descriptions of these caves and the bones of mammals found therein were published in a series of papers by Gerrit S. Miller (1922, 1926, 1929). Alexander Wetmore (1922) described some of the fossil birds, and Arthur J. Poole (1929) wrote additional descriptions of several more sites in the vicinity. Yet except for a comment on lizards by Hecht (1951) and Rímoli's (1976) review of the fossil rodents of Hispaniola, almost nothing has been written on the fossil material since its initial discovery.

All of the fossils and unsorted matrix from the St. Michel caves that were collected in the 1920s had been deposited with the Division of Vertebrate Paleontology, National Museum of Natural History, Smithsonian Institution. Some of the matrix remained in two shipping crates, each bearing a hand-written label identifying the contents as "small material from caves of Haiti, contains small shells, lizard jaws, etc. Has been sorted for small mammal remains." Each label had been initialed "P," presumably for Arthur J. Poole. Inside one crate was a note stating "Cave 1. Discarded material carefully worked over—Poole." "Cave 1" possibly refers to the first of three caves that Poole (1929:59) called the "San Francisco group . . . situated about three miles to the west of L'Atalaye and about one mile east of the village of St. Michel." While casually picking through this matrix recently I found that most of the fossils of mammals and birds had indeed been removed, yet abundant remains of lizards were still present. Among them were bones of the iguanid lizard *Leiocephalus*, a genus endemic to the West Indies and presently confined to the Greater Antillean Islands of Cuba, Hispaniola, and the Bahamas. Elsewhere in the West Indies at least five extinct species are known: Jamaica (Etheridge 1966a), the Dominican Republic (Etheridge 1964), Puerto Rico (Pregill 1981), and the Leeward Islands of Barbuda, Antigua and Anguilla (Etheridge 1964; Pregill, in prep.).

The fossils from St. Michel share certain similarities with the extinct species *Leiocephalus apertosulcus* that was described by Etheridge (1965), based on material collected from cave deposits in the Cerro de San Francisco, La Estrellata

Province, Dominican Republic. Yet consistent differences are apparent, especially in the partially closed Meckel's groove in the St. Michel lizards. The dentary is structurally intermediate between the completely open groove of *L. apertosulcus* and the closed and fused condition obtained in all other species of the genus. These and other features of this new *Leiocephalus* are described below.

Measurements were made with an eyepiece reticle on a Wild M8 stereomicroscope and read to the nearest 0.1 mm. Comparative skeletal material of *Leiocephalus* included representatives of 20 of 22 living species in the collections of the National Museum of Natural History, Smithsonian Institution (USNM), Museum of Comparative Zoology (MCZ), and Richard Etheridge (REE—San Diego State University). Notes and measurements on all fossil species of *Leiocephalus* were available from a previous study (Pregill 1981); the type material of *L. apertosulcus* was in hand. Estimates of snout to vent length of fossil individuals, hereafter referred to as SVL, are derived from the simple procedure of comparing ratios of measurements with modern individuals of known size (Pregill 1981).

Leiocephalus anonymus, new species

Fig. 1

Holotype.—USNM 340182, a right dentary in the collection of the Division of Vertebrate Paleontology.

Locality and horizon.—An unspecified cave(s) near St. Michel de l'Atalye, Département L'Artibonite, Haiti. Probably collected by Arthur J. Poole in December, 1927, in cave sediment of undetermined age, certainly no older than latest Pleistocene.

Etymology.—Greek, *anonymus*, nameless; in reference to the fact that fossils of this species lay buried in a crate for over fifty years, unnamed and unknown.

Referred material.—Dentaries: the type plus 18 left, 8 right nearly complete, and 30 fragments (USNM 340183–340185); Maxillae: 7 left, 7 right plus 17 fragments (USNM 340186–340188); Premaxilla: 1 (USNM 349192); Frontals: 5 complete and 3 partial (USNM 340189); Parietal: 1 (USNM 340190); Pterygoid: 1 partial right (USNM 34191).

Diagnosis.—A large species of *Leiocephalus* having Meckel's groove open except for a short distance in the middle of the dentary, usually between the twelfth and fifteenth teeth where the upper and lower borders converge and touch. The open portions of Meckel's canal expose a well-developed intramandibular septum. The pineal foramen is located wholly within the frontal bone.

Description of Holotype.—Tooth row 15.2 mm; length overall 18.6 mm, and height posterior to last tooth 3.4 mm; 24 pleurodont teeth of which numbers 5, 7, 8, 10 and 18 missing, front to back; estimated snout to vent length of individual in life 120 mm.

Teeth 1 through 4 plus number 6 simple, recurved and pointed; each slightly larger than tooth preceding; ninth tooth with small central cusp distinct from tooth shaft, and incipient lateral cusp on posterior side; tenth tooth and all those posteriad except for number 11 (missing crown) and number 24 (replacement tooth) with tricuspid crowns in fleur-de-lis shape typical of *Leiocephalus*. Anterior cusp of each tooth generally overlapping slightly posterior cusp of preceding tooth; shafts parallel-sided; approximately 35% of each tooth protruding above parapet

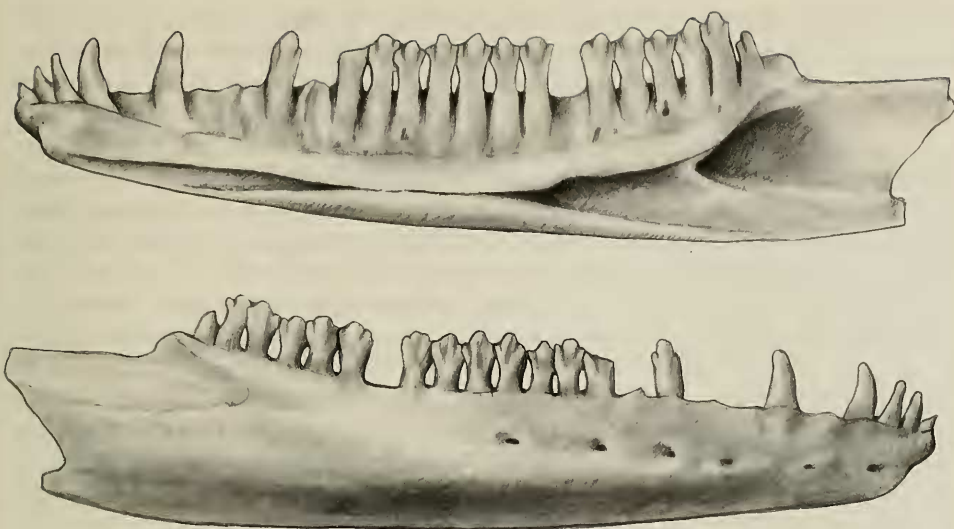


Fig. 1. Holotype of *Leiocephalus anonymus*, new species, a right dentary (USNM 340182) in lingual (above) and labial (below) view.

of jaw; teeth on holotype more abraded than those of some referred dentaries but their tricuspid condition clearly evident; on mesial side of dentary below dental shelf, Meckel's groove exposed anterior to twelfth tooth and posterior to fifteenth; between twelfth and fifteenth teeth, upper and lower borders of Meckel's groove converge and make contact, but do not fuse; within Meckel's canal well-developed intramandibular septum extending from symphysis posterior to level of last tooth; septum deeply emarginate at its posterior border.

Labial face of dentary convex throughout most of its length except for antero-ventral surface, where it is moderately flattened; horizontal row of six mental foramina perforating upper half of labial face between second and fourteenth teeth; in front of surangular process on dorsolabial surface, a deep wedge-shaped scar extending forward to level of twenty-second tooth, marking former position of anterolabial arm of coronoid.

Other dentaries.—Twenty-six other dentaries referred to this species are similar to the holotype in most respects. Some of these are nearly complete, others are badly worn, missing teeth or various processes and borders. Teeth missing from the holotype are present collectively on the referred specimens. The transition from simple to tricuspid teeth takes place rather abruptly between teeth 9 and 11. The number of teeth increases ontogenetically from 19 in the smallest dentary (tooth row of 9.2 mm) to 25 in the largest (tooth row 16.4 mm). These dentaries came from individuals estimated at 73 mm and 130 mm SVL, respectively. The average tooth row length for the 26 dentaries is 13.9 mm, an individual of approximately 110 mm SVL. The scar of the coronoid overlap on the dorsolabial surface spans a distance equivalent to 1 to 4 posteriormost teeth ($\bar{x} = 2.1$), and the number of mental foramina ranges from 4 to 8 ($\bar{x} = 5.5$) placed between the second and fourteenth teeth.

The most important diagnostic feature is the persistence of a partially closed

Meckelian groove near the middle of the dentary. In most cases contact is made between the upper and lower borders of Meckel's groove; in three specimens the borders actually fuse, and in two specimens Meckel's groove is continuously open.

Maxillae.—Fourteen nearly complete maxillae have tooth rows ranging from 11.3 mm (93 mm estimated SVL) to 15.4 mm (126 mm estimated SVL). The average tooth row length is 13.4 mm (110 mm estimated SVL). Tooth counts vary from 18 to 22, the number increasing with the size of the jaw. In all specimens the transition from simple to tricuspid teeth takes place at the eighth or ninth tooth. The teeth are otherwise similar to those on the dentary.

The supradental shelf is curved medially at the anterior end where it forms the premaxillary process. A prominent palatine process protrudes medially just posterior to the middle of the shelf. On the labial side of the maxilla a tall nasal process rises almost vertically above the dental row. Anterodorsally, the nasal process turns sharply mediad above the fenestra exonarina. On the nasal process immediately above the tooth row is a horizontal series of from 6 to 9 maxillary foramina placed between the third and thirteenth teeth. In one specimen the foramina are placed between the second and eleventh teeth. An additional 1 to 3 foramina penetrate the nasal process above the first 2 to 6 maxillary foramina.

Premaxilla.—A single premaxilla is referred to this species by its large size, and similarity to the premaxilla of other *Leiocephalus*. The rectangular incisive process is 3.6 mm wide, and bears seven simple, pointed teeth, as in all species of the genus. There is minimal inflection between the incisive process and the posteriorly directed nasal process, which is 1.4 mm wide at its base and 3.9 mm in length. The nasal process is thus relatively narrow and long in comparison to that of other species such as *L. carinatus*.

Frontal.—Five of the frontal bones are nearly complete; three others are missing portions of the postfrontal or nasal processes. The largest has a midsagittal length of 12.1 mm, an interorbital width of 4.2 mm, and measures 12.2 mm across the parietal border. These same measurements on the smallest complete specimen are 9.9 mm, 3.3 mm, and 9.5 mm, respectively. Overall, the frontal bone of *L. anonymus* has a gentle dorsal curvature with a rugose surface. In all specimens the pineal foramen lies wholly within the frontal bone, near the middle of the parietal border. Two deep semicircular excavations anteriorly indicate the former overlap of the nasal bones.

Ventrally, the olfactory canal is a smooth, deep fossa occupying the anterior third of the bone and bordered on either side by sharply descending subolfactory processes.

Parietal.—The single parietal referred to this species is missing only the distal half of the left supratemporal process. Its width at the frontal border is 10.2 mm. The width across the ends of the supratemporal processes is approximately 12.7 mm, accounting for the broken left tip. The midsagittal length is 4.7 mm. The bone probably came from a subadult individual estimated at 97 mm SVL.

The parietal table is rugose, like the frontals, and the sides converge postero-medially above the parietal fossa. On each of the anterolateral processes there is a distinct notch that in life articulates with the postorbital.

Pterygoid.—A single right pterygoid is missing the distal half of the quadrate process but otherwise is complete. There are no pterygoid teeth. The bone measures 5.9 mm across the tips of the palatine and ectopterygoid processes. A deep

basipterygoid notch is present for articulation with the basipterygoid process of the basisphenoid. In *Leiocephalus* the basipterygoid notch is accentuated by a pronounced ventral shelf and the ectopterygoid process is excavated on the dorsomedial surface.

Remarks.—Because of the unusual form of the dentary, *Leiocephalus anonymus* need only be distinguished from the extinct species *L. apertosulcus*. Indeed, one might argue that *L. anonymus* is simply a population of *L. apertosulcus* in which Meckel's groove has become partially closed. But the two differ in other respects, and some features stand apart as much or more than those of other *Leiocephalus*. Unfortunately, only a few comparably diagnostic bones are known for both taxa. For example, the premaxilla is unknown in *L. apertosulcus* but most other major skull elements have been identified (Etheridge 1965). In *L. anonymus* the premaxilla is known, but the species is otherwise represented by comparatively few cranial bones. For now, whether or not these two species are each other's closest relatives is an interpretation that depends largely on whether the open condition of Meckel's groove is primitive or derived.

In all species of *Leiocephalus* Meckel's groove is closed and fused except for a small opening anteriorly. In two fossil species, *L. etheridgei* and *L. partius* (both from Puerto Rico), Meckel's groove is open anteriorly as a narrow sulcus extending back a distance of 5 to 6 teeth (Pregill 1981). Of fifty dentaries referred to *L. apertosulcus* by Etheridge (1965) a continuously open groove was present in all but two specimens, wherein the upper and lower borders of the groove made contact below the twelfth to fourteenth teeth. Both species have a well-developed intramandibular septum (IMS), a structure found in other *Leiocephalus* only in the extinct species *L. partitus*, and the Antigua Bank form *L. cuneus*. Loss of the IMS in *Leiocephalus* and other tropidurines is thought to be a derived state correlated with closure and fusion of Meckel's groove (Pregill 1981). However, the septum is present in *L. partitus* and *L. cuneus*, two species having the Meckelian groove closed. In these, the persistence of the IMS may be the result of a reversal secondarily derived, or simply a retention of the primitive condition. I prefer the former interpretation because the complex dentary/postdentary articulation is constructed about a closed septumless Meckel's groove in most tropidurines and all extant *Leiocephalus*, clearly a monophyletic genus (Etheridge 1966b; Pregill, in prep.). By this same reasoning, the open and nearly open groove of *L. apertosulcus* and *L. anonymus* may also be a reversal and thus a shared derived character. However, Etheridge and de Queiroz (in prep.) suggest that an open Meckel's groove is plesiomorphic for iguanids. Hence, the character polarity of an open Meckel's groove and the presence of an intramandibular septum in *Leiocephalus* is still conjectural. (A review of the various tropidurine genera under way by Richard Etheridge, Darrel Frost, and myself may cast light on this interesting character complex.)

Another feature in which *L. anonymus* differs from *L. apertosulcus* is that the pineal foramen is located completely within the frontal bone. In *L. apertosulcus* and all other species except *L. semilineatus* and *L. raviceps*, the foramen is located at the frontoparietal suture, the primitive condition for iguanids (Etheridge and de Queiroz, in prep.) By comparison to *L. apertosulcus*, the frontal of *L. anonymus* is also proportionately wider between the orbits. This can be confirmed by visual inspection, and verified by comparing their ratios of interorbital width to mid-

sagittal length. The ratio averages 0.350 (0.339–0.377) in the five complete frontals of *L. anonymus*, and 0.315 (0.300–0.329) in frontals of *L. apertosulcus*. In fact, the difference in these ratios increases ontogenetically in this sample of individuals, estimated at from 85 mm to 130 mm SVL.

Differences also exist in the shape of the supratemporal processes of the parietal. In *Leiocephalus* the sides of the parietal table converge posteromedially with increased body size (Etheridge 1966b), whereas the shape of the supratemporal processes remains more or less unchanged during growth. Those of *L. apertosulcus* are flared dorsoventrally and are deeply emarginate; in *L. anonymus* the processes are narrower and not as excavated.

Differences in the maxilla and pterygoid bones between these two species are subtle; in fact, neither bone varies significantly among *Leiocephalus*. Pterygoid teeth are absent from both, but they have also been lost in most other species of the genus. The maxillae differ principally in that the transition to tricuspid teeth takes place variably between teeth 5 and 8 in *L. apertosulcus*, and rather abruptly at tooth 8 or 9 in *L. anonymus*. The transition to tricuspid teeth in *Leiocephalus* is subject to some ontogenetic increase (i.e., more posteriad), but there is an observable pattern throughout the genus. In some species the transition is consistently anterior at about the fourth or fifth tooth, as in *L. cuneus*. In other species such as *L. cubensis* the transition is as far posteriad as the tenth or eleventh tooth. The latter is probably the more derived condition (Pregill, in prep.).

Leiocephalus apertosulcus may have obtained a larger maximum adult size than *L. anonymus*. My calculations concur with Etheridge's estimates that *L. apertosulcus* was at least 150 mm snout–vent length, and possibly as much as 200 mm. *Leiocephalus anonymus*, on the other hand, probably obtained an average maximum size between 120 and 130 mm SVL. These figures may be influenced by sampling bias in the fossil record. It is curious, however, that both these species plus the other extinct forms *L. jamaicensis* and *L. cuneus* achieved a snout–vent length greater than any living species. Among living members only *L. carinatus* and *L. melanochloris* approach 120–130 mm.

Characters in which the two species are similar include the transition to tricuspid teeth on the dentary, the length of the coronoid overlap on the dentary's dorsolabial surface, and the number of mental and maxillary foramina. Of these, only the transition to tricuspid teeth has any phylogenetic utility. The other features vary individually and ontogenetically within *Leiocephalus* and are of little or no use as systematic characters. As with maxillary teeth, the transition to tricuspid teeth on the dentary occurs as far anteriorly as the third or fourth tooth in some species, and posteriorly at the eleventh or twelfth tooth in others.

The distribution of *Leiocephalus* in the West Indies today is obviously relictual, yet the causes of extinction within the group are unclear. Some extinctions may be related to changes in climate and sea level at the end of the Pleistocene 10–12,000 years ago (Pregill and Olson 1981), whereas others are probably much more recent and due to environmental disturbances wrought by early human colonization in the Antilles (Steadman *et al.*, 1984). Neither Miller (1922, 1926, 1929) nor Poole (1929) speculated much about the ages of the bone-bearing sediments from St. Michel, but like all other cave deposits thus far known from the West Indies, they are certainly no older than Late Pleistocene. Supposedly, some of the St. Michel sites were at least pre-Amerindian, others apparently were

contemporaneous with early human occupation of the region. I did find bones of *Rattus* in the crates of matrix from which the fossils of *L. anonymus* were removed. Unfortunately, collecting techniques were often haphazard in earlier days and surface sediments could have been mixed with several deeper layers, or contaminated in other ways. Hence, we cannot be totally confident that *L. anonymus* actually survived into post-Columbian time, that is, after *Rattus* had been introduced. A recent extirpation is not unlikely in view of the compelling evidence for human-caused extinction of small vertebrates in the West Indies (Steadman *et al.*, 1984).

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